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A guide to the Ovarian Histology of Pacific Cod

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ABSTRACT

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The development of the ovary of Pacific cod (Gadus macrocephalus) was examined macroscopically and by microscopic cross section. Oocyte growth and development were recorded by photomicrography for correlation with macroscopic maturity stages of the ovary. Characteristics were described for each maturity stage. A glossary of commonly encountered terms was compiled for use in future investigations of reproductive biology of fishes.

RÉSUMÉ

Bowden, D. G., R. P. Foucher and A. V. Tyler. 1990. A guide to the ovarian histology of Pacific cod. Can. Tech. Rep. Fish. Aquat. Sci. 1723: 44 p.

La développement des ovaires chez la morue du Pacifique (Gadus macrocephalus) a été étudié à l'échelle macroscopique et au moyen de coupes microscopiques. L'accroissement et le développement des ovocytes ont été enregistrés par photomicrographie afin d'établir des corrélations avec les stades macroscopiques de maturité de l'ovaire. Des caractéristiques ont été décrites pour chacun des stades de maturité. Un glossaire des termes d'usage courant a été établi en vue des prochaines études sur la biologie de la reproduction des poissons.

INTRODUCTION

Pacific cod (Gadus macrocephalus) is a major component of the bottom-trawl fishery in British Columbia (Tyler and Foucher 1989). Studies on the biology of Pacific cod at the Pacific Biological Station include the investigation of reproductive mechanisms and cycles and attempts to predict recruitment.

The literature was reviewed for information dealing with oogenesis and reproduction in Pacific cod. Two problems surfaced as a result of this search: first, a lack of literature dealing with reproduction of Pacific cod; and excess variation in the terminology used for the description of oogenesis. The latter problem is discussed in several papers (Hurley and Fisher 1966; Anderson 1967; Laale 1980; Groot and Alderdice 1985). The process of oogenesis is well documented for several species (Aravindan and Padmanabhan 1972; Foucher and Beamish 1977, 1980; Negonovskaya 1982; Robb 1982; Hay et al. 1987; Selyukov 1987).

This paper was initiated in response to the need for an accurate and concise guide to ovarian development, at both the macroscopic and microscopic levels, in Pacific cod. However, this paper does not cover folliculogenesis or the biochemical and molecular aspects of oogenesis. These topics are covered in great detail by Guraya (1986) and Detlaff and Vassetsky (1988).

MATERIALS AND METHODS

Pacific cod were caught by otter trawl in Hecate Strait, (Figure 1), on the northwest coast of British Columbia during 1987/88 and off Ucluelet, on the west coast of Vancouver Island in 1988. Gonad maturity was determined macroscopically according to a maturity index (Table 1). Ovary samples were dissected and fixed in buffered formal saline solution, (130 g Na_2HPO_4, 80 g NaH_2PO_4, 180 g NaCl, 2 l formalin and 18 l water). Fish length (fork length to the nearest cm), ovary maturity and identifying fish number of each fish used for histology are given in Table 2a. Additional fish were photographed to show macroscopic gonad maturity stages (Table 2b). Fish numbers are used to identify the source of ovary tissue in the figures.

Tissue from the middle section of the ovary was embedded, sectioned at five micrometers, processed using routine histological techniques and stained with Harris' haematoxylin-eosin (Yasutake and Wales 1983). Prepared sections were examined

to determine features, on the microscopic level, characteristic for maturity stages assigned at the macroscopic level, then photographed. The oocyte size distributions for each maturity stage were determined by direct measurement of an image of the section projected by a scale projector. Only those oocytes whose nuclei were included in the sections were measured (Foucher and Beamish 1980).

RESULTS

The gonads of Pacific cod are paired structures located posterio-ventrally in the body cavity (Figure 2). They open externally via the abdominal pore located anterior to the first anal fin. The ovary is widest near the middle section, while the anterior portion is wider than the posterior section (Figure 2a). The testes of a ripe male are highly convoluted and fill the posterior half of the body cavity (Figure 2b).

Macroscopic

Stage 1 ovaries (no Figure available) are immature and appear as translucent, string-like structures often difficult to locate within the body cavity. Stage 2 ovaries (Figure 3a.), also immature begin to show some coloration, but are still quite small. Beyond stage 2, ovaries are mature. A mature female goes through the cycle from stage 3 to stage 7 once in each spawning season. Stage 3 ovaries (Figure 3b) are large structures containing creamy-coloured oocytes. This stage is characterized by oocytes visible through the ovary wall and vascularization of the ovary. Stage 4 ovaries (Figure 3c) are creamy-coloured with oocytes visible through the thinning, translucent wall. Vascularization of the ovary wall is pronounced and the ovaries fill a large portion of the body cavity. Fish with stage 5 ovaries (Figure 3d) appear gravid and ova may flow from the abdominal pore if the fish is squeezed. During this stage the ovary wall is thin and appears stretched. Ova are visible and appear translucent. Stage 6 ovaries are flaccid and bloodshot. At this point most ova have been released but some translucent cells may remain in the ovary. Ovaries at stage 7 (Figures 3e,f) are characteristically small and black or silver in colour. The ovary wall is thick and firm. The black or silver coloration may not always appear or persist until the next stage 3. Stage 7 ovaries that lack this coloration can be confused with stage 2 ovaries. Ovaries of older fish are frequently black or black and silver in colour (Figure 4a,b). The silver colour is due to the presence of iridocytes within the peritoneal covering of the

ovary. These iridocytes contain guanine, a purine with highly reflective properties.

Microscopic

The stage 1 ovary (Figure 5a) has many well developed lamellae that project into the lumen. These lamellae are covered by a germinal epithelium that contains minute germ cells, small oocytes and larger, reserve-fund oocytes. Early in the stage 2 ovary (Figure 5b) some of the reserve-fund oocytes show signs of growth and vacuolization. By late stage 2 (Figure 5c) these vacuolated oocytes are predominant within the ovary. These large vacuolated oocytes develop an external oocyte membrane and a layer of follicle cells by the end of stage 2. These are readily distinguishable from the smaller non-vacuolated reserve-fund oocytes. The stage 3 ovary (Figure 5d) is characterized by the addition of a grey-coloured band around the nucleus of the vacuolated oocytes. The nature of this band is uncertain, but it may be associated with the Balbiani's vitelline body (see glossary). Vacuolated oocytes with this grey band enter a period of vitellogenesis early in the stage 4 ovary (Figure 5e). Yolk granules deposited during vitellogenesis greatly increase the volume of vitellogenic oocytes and this growth obscures the organization of the lamellae within the ovary. The late stage 4 ovary (Figure 5f) contains many large, vacuolated, yolk-filled oocytes. These oocytes appear to have small nuclei and lack the grey band, present in stage 3. Reserve-fund oocytes are encountered less frequently in ovary sections in advanced stages as they have been spread through a greater volume. The process of ovulation occurs in the stage 5 ovary (no Figure available). At this point the gametes are referred to as ova. A further increase in size occurs as the ova become hydrated just prior to spawning. The stage 6 ovary is spent but some translucent ova may remain within the ovary (Figure 5g). These cells are phagocytized by macrophages that proliferate within the ovary following spawning. There are also collapsed, empty follicles interspersed among the reserve-fund oocytes. These follicles are resorbed or form post-ovulatory corpora lutea. The characteristic features of stage 7 ovaries (Figure 5h) are more visible lamellae within the lumen and a thickening of the ovary wall. Reserve-fund oocytes dominate the germinal epithelium of the stage 7 ovary, but some vitellogenic oocytes may be present.

Frequency Distributions

Figures 6a-j show the frequency distributions of oocyte diameters for stages 1 through 7, excluding stage 5. From these histograms it is apparent that a mode of cells, approximately 50-150 microns in diameter, is present in all stages. This mode (Figure 6a) corresponds to the reserve-fund of oocytes. Early in stage 2 (Figure 6b) a second small mode appears. This group of

cells originates from reserve-fund oocytes entering the vitellogenic stage. By late stage 2 and stage 3 (Figure 6c,d) these two modes are readily distinguishable from one another. During stage 4 (Figure 6e) the mode of vitellogenic oocytes becomes more separated from the reserve fund as they increase in size. Vitellogenic oocytes in the late stage 4 ovary (Figure 6f) range from approximately 200-725 microns in diameter. Those oocytes nearing ovulation range from approximately 600-750 microns in diameter. At stage 5, ovulation occurs, ova undergo hydration and increase greatly in diameter. This stage is rarely seen and must persist for only a short while, just before spawning. At spawning, eggs are about 1.02 mm in diameter (Hart 1973). Following spawning in the early stage 6 ovary (Figure 6g) a single mode of cells remains, corresponding to the reserve-fund. The frequency distributions of oocytes in late stage 6 (Figure 6h) and stage 7 ovaries (Figure 6i) resemble those of stages 1 and 2.

Oocyte Growth and Development

Cells in the stage 1 ovary range from minute germ cells and oogonia to larger previtellogenic oocytes. Germ cells and oogonia have large nuclei that occupy much of the cell's volume (Figure 7a). The oogonia divide mitotically to produce small oocytes. In material we have examined, the nuclei of these oocytes were characteristically located to one side of the cell (Figure 7a). This has also been observed for trout (Negonovskaya 1982). Many dense nucleolar structures appear throughout the nuclei of such oocytes. As an oocyte increases in diameter, its nucleus moves to the centre of the cell and the nucleoli arrange around the periphery of the nucleus (Figures 7b-c). These nucleoli are often referred to as euvitelline nucleoli (see glossary). These large, previtellogenic oocytes form much of the reserve-fund in the stage 1 ovary. Some of these reserve-fund oocytes show signs of vacuolization early in stage 2 (Figure 7d). The presence of these vacuoles indicates the initiation of major oocyte growth. By late stage 2 a band of large vacuoles occupies the periphery of the cytoplasm (Figure 7e). A layer of follicle cells and an external oocyte membrane appear late in stage 2. These structures are well developed by stage 3 (Figure 7f). Appearing at this point is a grey-staining band that envelopes the nucleus. The nature and function of this band is questionable, however, it may be associated with the "yolk nucleus" or Balbiani's vitelline body. Oocytes possessing this so-called "yolk nucleus" are vitellogenic and accumulate compact yolk granules (Figure 7g). By late stage 4 the "yolk nucleus" is no longer apparent and the yolk granules begin to coalesce with the cell's cytoplasm (Figure 7i,j). At ovulation, early in stage 5, oocytes are released from their nutritive follicles and become ova. Ovulation is followed by cell hydration, whereby the ova increase greatly in volume just prior to being released at

spawning. Any unspawned oocytes or ova are quickly resorbed (Figure 7j). Some larger oocytes that never reached the stage of hydration develop invaginations of the external oocyte membrane (Figure 7k) indicating that resorption is underway. Late in stage 6, the ovary may have many resorbing oocytes referred to as atretic bodies (Figure 7l). Phagocytic macrophages proliferate within the stage 6 ovary. These cells "clean" the ovary of all disrupted oocytes and ova. In association with the appearance of macrophages, the fibrous material of the ovary takes on a black coloration. This coloration is caused by the accumulation of melanin granules deposited by the macrophages. Collapsed follicles litter the ovary, sometimes forming corpora lutea. These structures are short-lived and, while in mammals they have a secretory function, in fish they are "of doubtful endocrine function" (Jones 1978). There have been suggestions that some cells of these structures may differentiate to form new oogonia. See Foucher and Beamish (1977) for a discussion of this question. Whatever their source, new oogonia undergo synapsis and develop into post-synaptic cells (Figure 7m). They then add cytoplasm and grow to join the reserve fund of oocytes replacing those that developed for the previous season's spawning. However, many of the follicle cells simply die off. These cells have characteristically dark nuclei (Figure 7n) and are referred to as pycnotic (personal communication from J. Bagshaw, histologist, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.).

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Table 1. Expanded description of the maturity stages for female Pacific cod.

Stage	Maturity	Description[a]
1	Immature	Ovaries small, white, somewhat translucent, little more than smooth, clear strings from anterior origin to oviduct, sometimes thickening.
2	Immature (Maturing)	Ovaries small, but with definite elongated shape. May be becoming pinkish. No visible oocytes or prominent blood vessels. Diameter usually less than 2 cm. Still occur in fish in 40-50 cm range and occasionally larger.
3	Early ripe (Mature)	Ovaries large, opaque, creamy orange. Blood vessels prominent. Ovary size depends on size of fish but likely to be at least 1 cm in diameter by 5 cm in length, larger in older fish. Oocytes may be visible, at least if ovary is cut. May have some black or silver colouring to ovary wall if fish has spawned previously. Unlikely to occur in fish below 40 cm.
4	Late ripe (Mature)	Ovaries large, oocytes visible, creamy-yellow. Ovary size could be 3 or 4 cm or larger in diameter and 10 or more cm in length. Individual oocytes visible through any translucent parts of the ovary wall. May contain a few translucent eggs.
5	Running ripe (Mature)	Ovaries very large, each ovary from a large fish may be 1 litre in volume. Externally, the fish will look obviously gravid. Ovary wall with thin, stretched appearance. Most eggs translucent. Eggs may flow from vent if fish is squeezed.
6	Spent (Mature)	Ovaries medium in outline but flaccid. Flaccid condition probably does not last long. Ovaries dark and bloodshot with reddish-brown interior. May be a few translucent eggs remaining.
7	Resting (Mature)	Ovaries small, firm, may have some black or silver colour.

[a]Adapted from Westrheim 1977.

Table 2a. Fish length and gonad maturity of female Pacific cod used for histology and oocyte frequency distributions.

Fish no.	Date (yymmdd)	Location	Length (cm)	Maturity stage
26	870110	White Rocks	68	4[a]
1	870317	Ole Spot	72	4[b]
4	870317	Ole Spot	52	2[a]
23	870317	Ole Spot	64	6[a]
10	870608	Two Peaks	38	1
6	870826	Horseshoe	62	2[b]
57	871104	White Rocks	54	3
9	880309	South Bonilla	66	7
16	880309	South Bonilla	66	6[a]
37	880422	Amphitrite	61	6[b]

[a] Early.
[b] Late.

Table 1b. Fish length and gonad maturity of Pacific cod used for macroscopic stages.

Date (yymmdd)	Location	Sex	Length (cm)	Maturity stage
840130	White Rocks	female	44	2
840223	White Rocks	female	65	4
840223	White Rocks	female	68	5
841107	Two Peaks	female	68	7
881207	Victoria	female	62	3
881207	Victoria	male	62	-

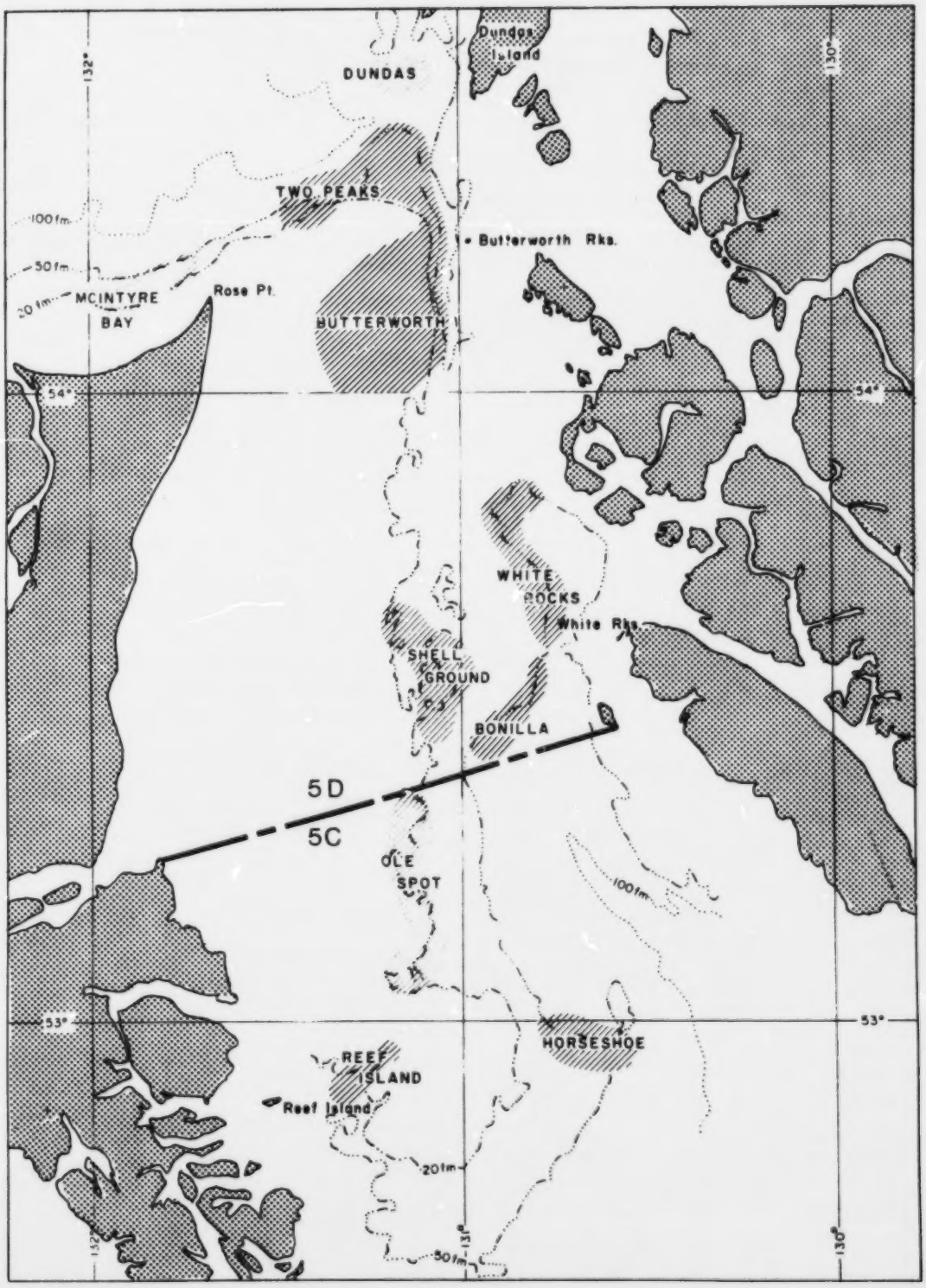
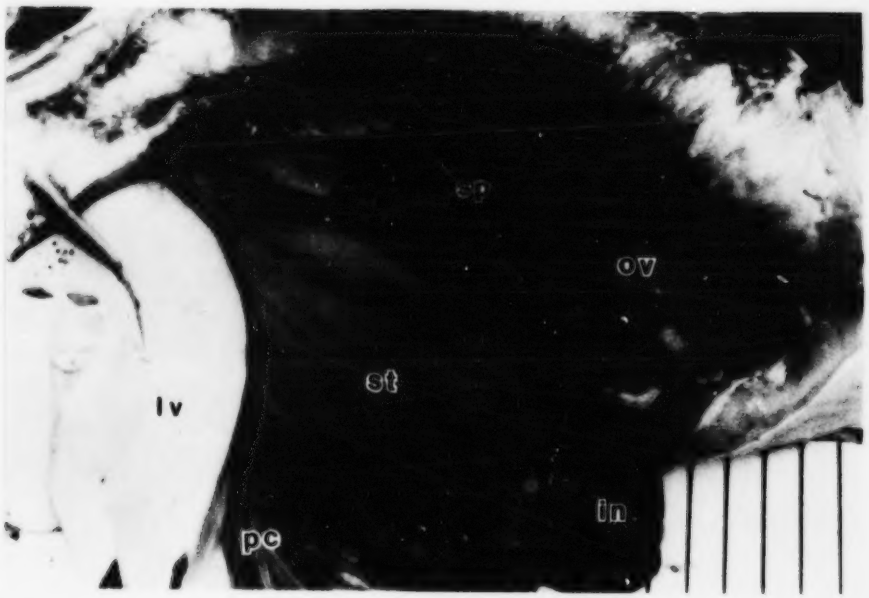


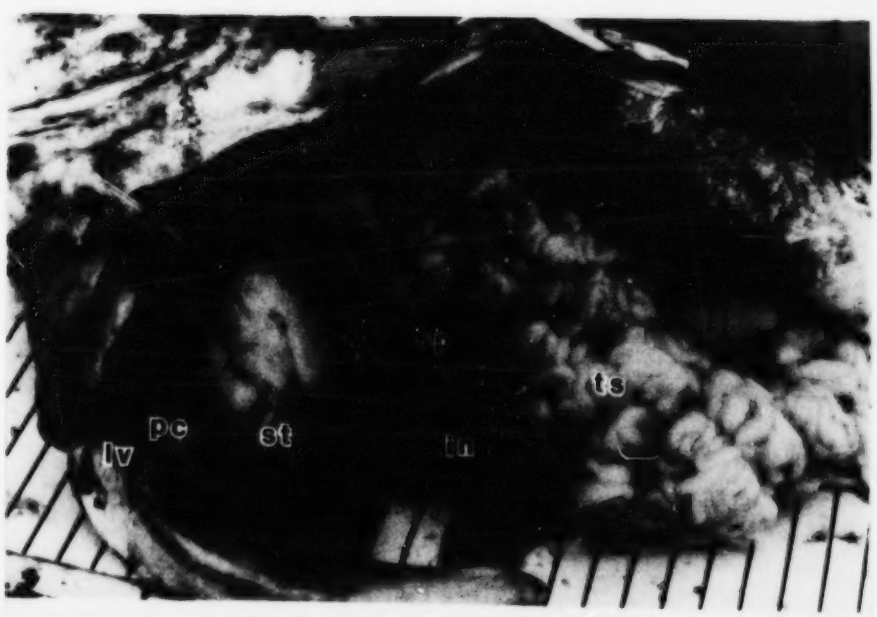
Figure 1. Trawling grounds for Pacific cod in Hecate Strait.

Figure 2a. Female Pacific cod: visceral anatomy.
(lv) liver, (pc) pyloric caecae, (st) stomach, (sp) spleen, (in) intestine, (ov) ovary

Figure 2b. Male Pacific cod: visceral anatomy.
(lv) liver, (pc) pyloric caecae, (st) stomach, (sp) spleen, (in) intestine, (ts) testis



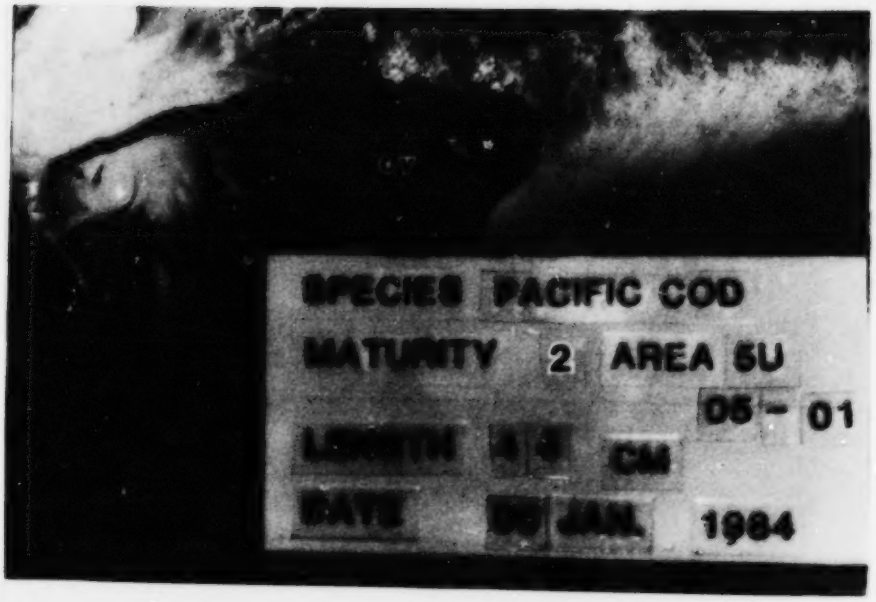
a



b

Figure 3a. Stage 2 ovary: macroscopic.
(ov) ovary

Figure 3b. Stage 3 ovary: macroscopic.
(ov) ovary, (bv) blood vessels



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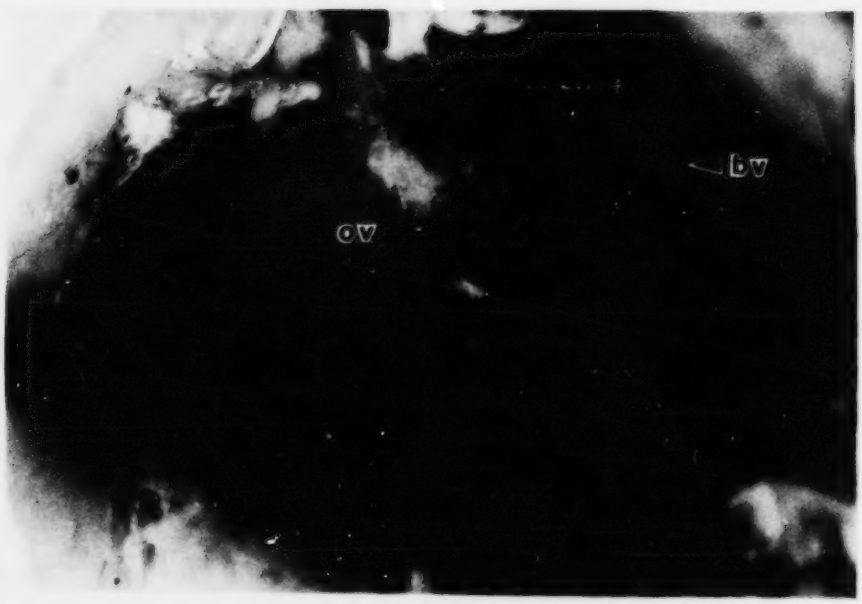

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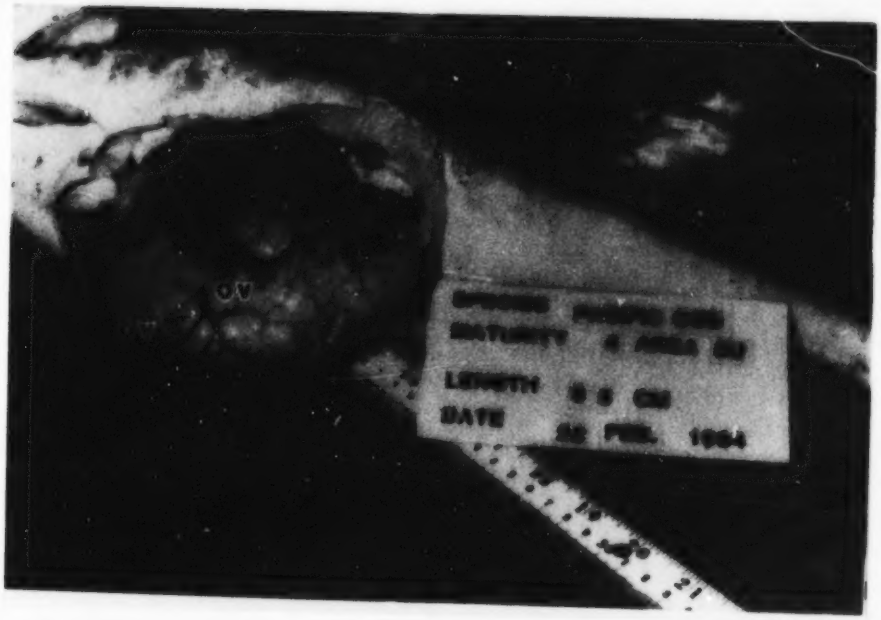
Figure 3c. Stage 4 ovary: macroscopic.
(ov) ovary, (bv) blood vessels

Figure 3d. Stage 5 ovary: macroscopic.
(ov) ovary


LENGTH
DATE

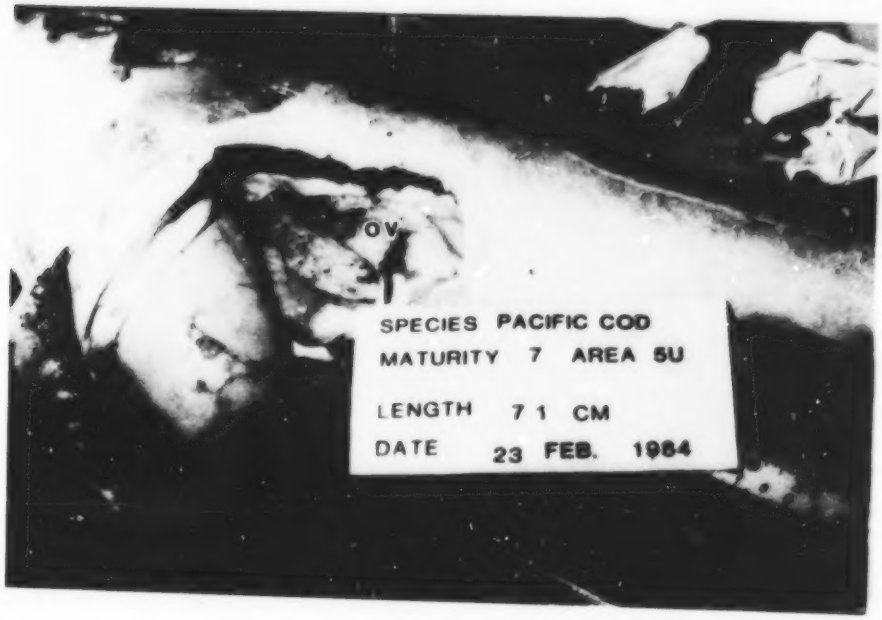
c

SPECIES PACIFIC COD
MATURITY 5 AREA 5U
LENGTH 68 CM
DATE 23 FEB. 1984

d

Figure 3e. Stage 7 ovary (early): macroscopic.
(ov) ovary showing black patches caused by melanin granules.

Figure 3f. Stage 7 ovary (late): macroscopic.
(ov) ovary showing black coloration caused by melanin granules.


OV
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MATURITY 7 AREA 5U
LENGTH 71 CM
DATE 23 FEB. 1984

e

OV
SPECIES PACIFIC COD
MATURITY 7 AREA 1E
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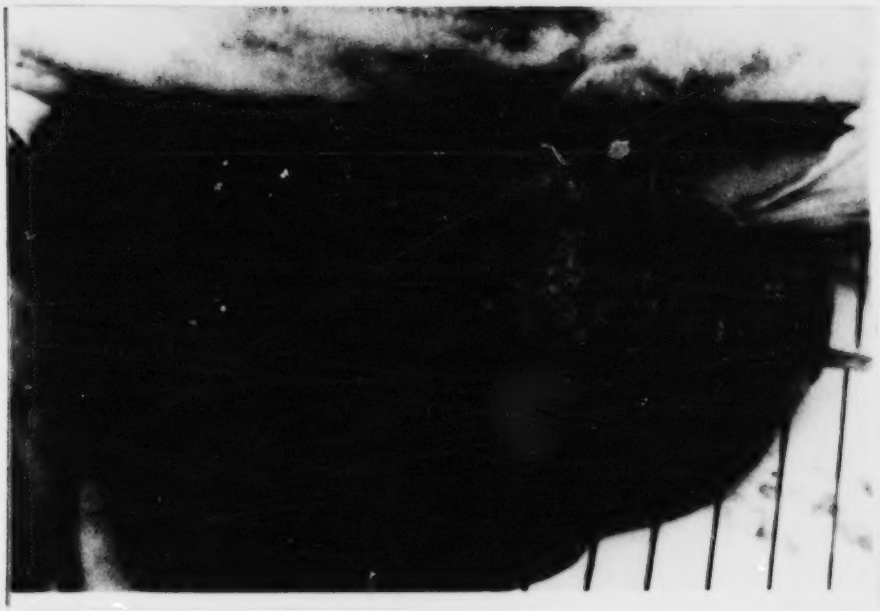
LENGTH 68 CM
DATE NOV. 7 1984

f

Figure 4a. Stage 3 ovary (macroscopic) showing black coloration of ovary wall.

Figure 4b. Stage 3 ovary (macroscopic) cut to show oocytes internally. This is the same ovary as in Figure 4a. (oc) oocytes, (ow) ovary wall



a

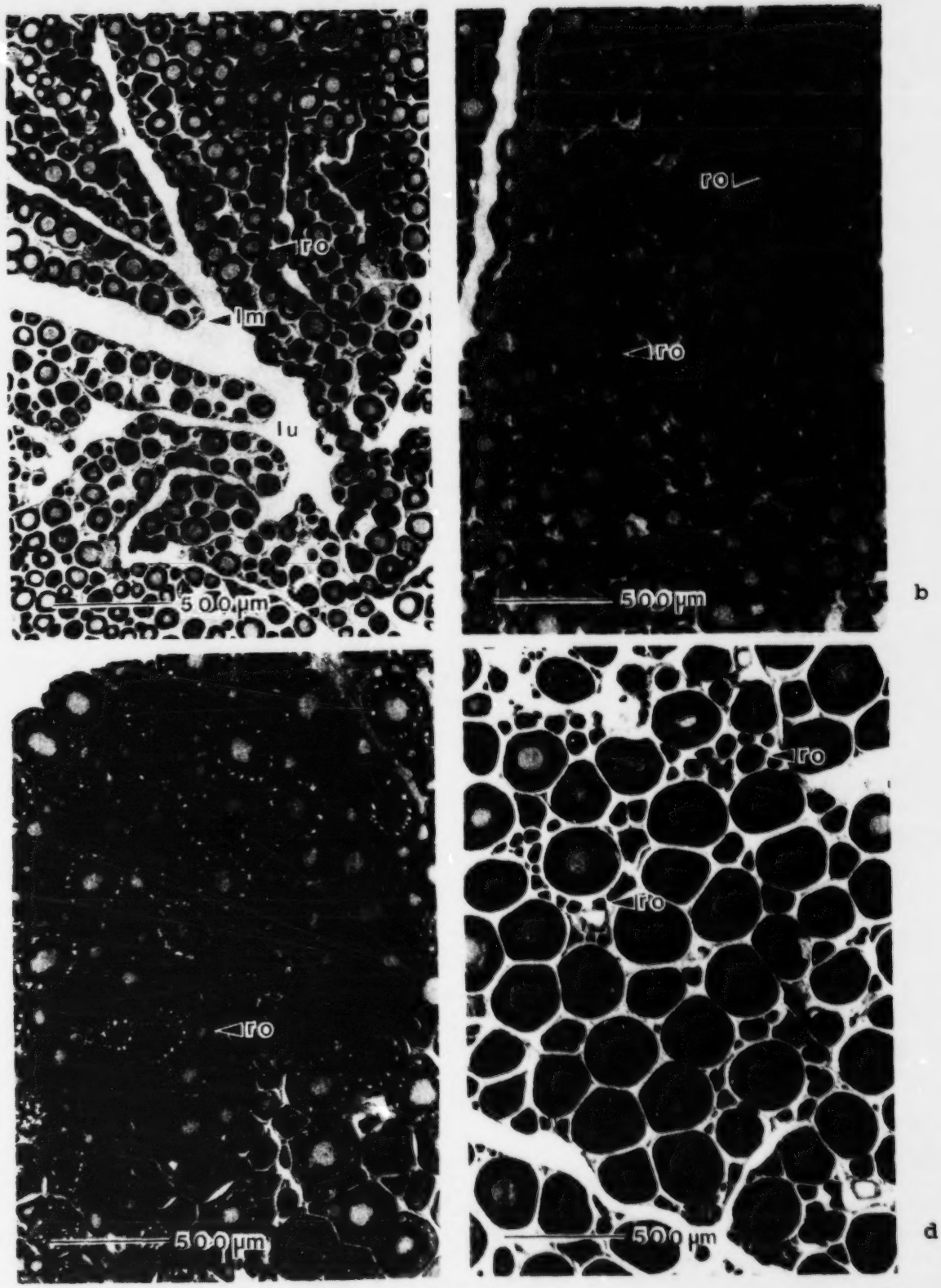
b

Figure 5a. Cross section of stage 1 ovary. Fish no. 10.
(lm) lamella, (lu) lumen,
(ro) reserve-fund oocyte

Figure 5b. Cross section of early stage 2 ovary. Fish no. 4
(ro) reserve-fund oocyte

Figure 5c. Cross section of late stage 2 ovary. Fish no. 6
(ro) reserve-fund oocyte

Figure 5d. Cross section of stage 3 ovary. Fish no. 57
(ro) reserve-fund oocyte


ro
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500 µm
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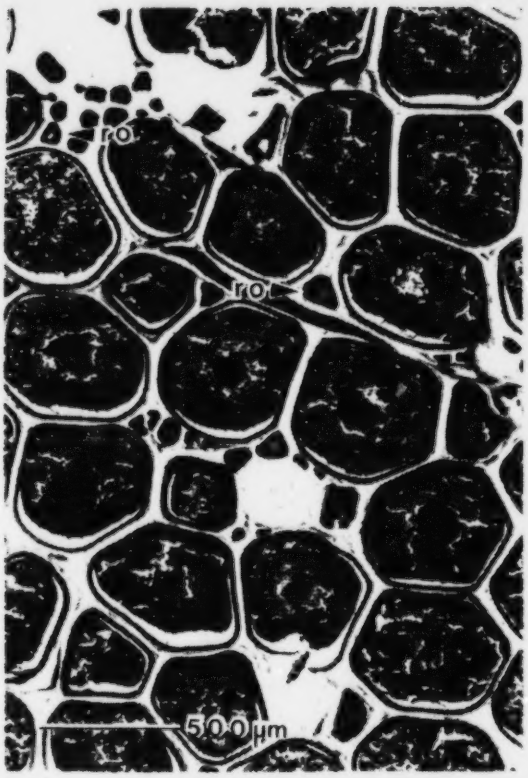
ro
500 µm
c
ro
ro
500 µm
d

Figure 5e. Cross section of early stage 4 ovary. Fish no. 26
(ro) reserve-fund oocyte

Figure 5f. Cross section of late stage 4 ovary. Fish no. 1
(ro) reserve-fund oocyte

Figure 5g. Cross section of early stage 6 ovary. Fish no. 16
(fc) follicle, (ov) ovum,
(ro) reserve-fund oocyte

Figure 5h. Cross section of stage 7 ovary. Fish no. 9
(lm) lamella, (lu) lumen, (ow) ovary wall
(ro) reserve-fund oocyte



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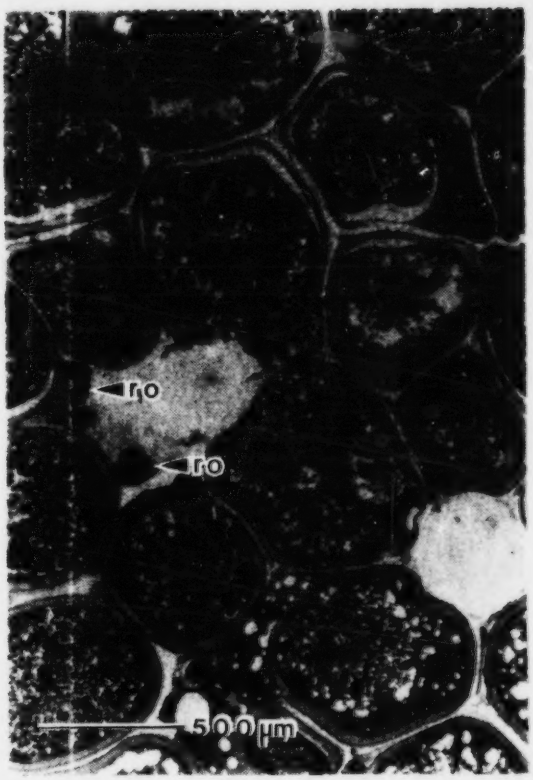

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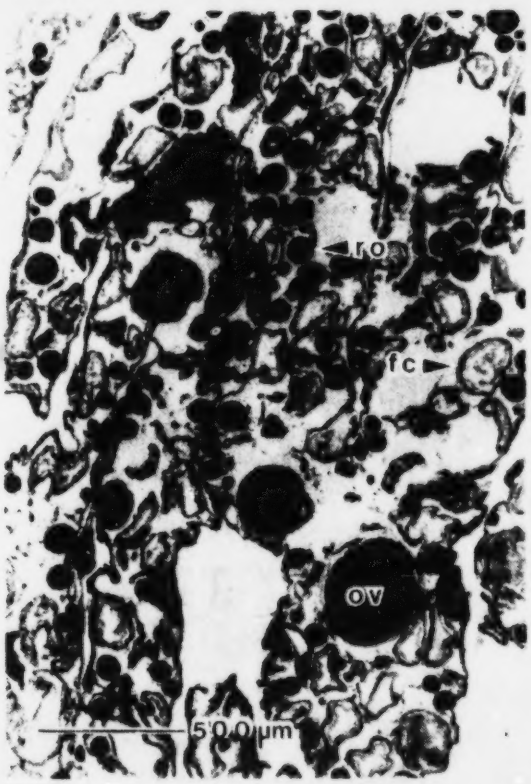

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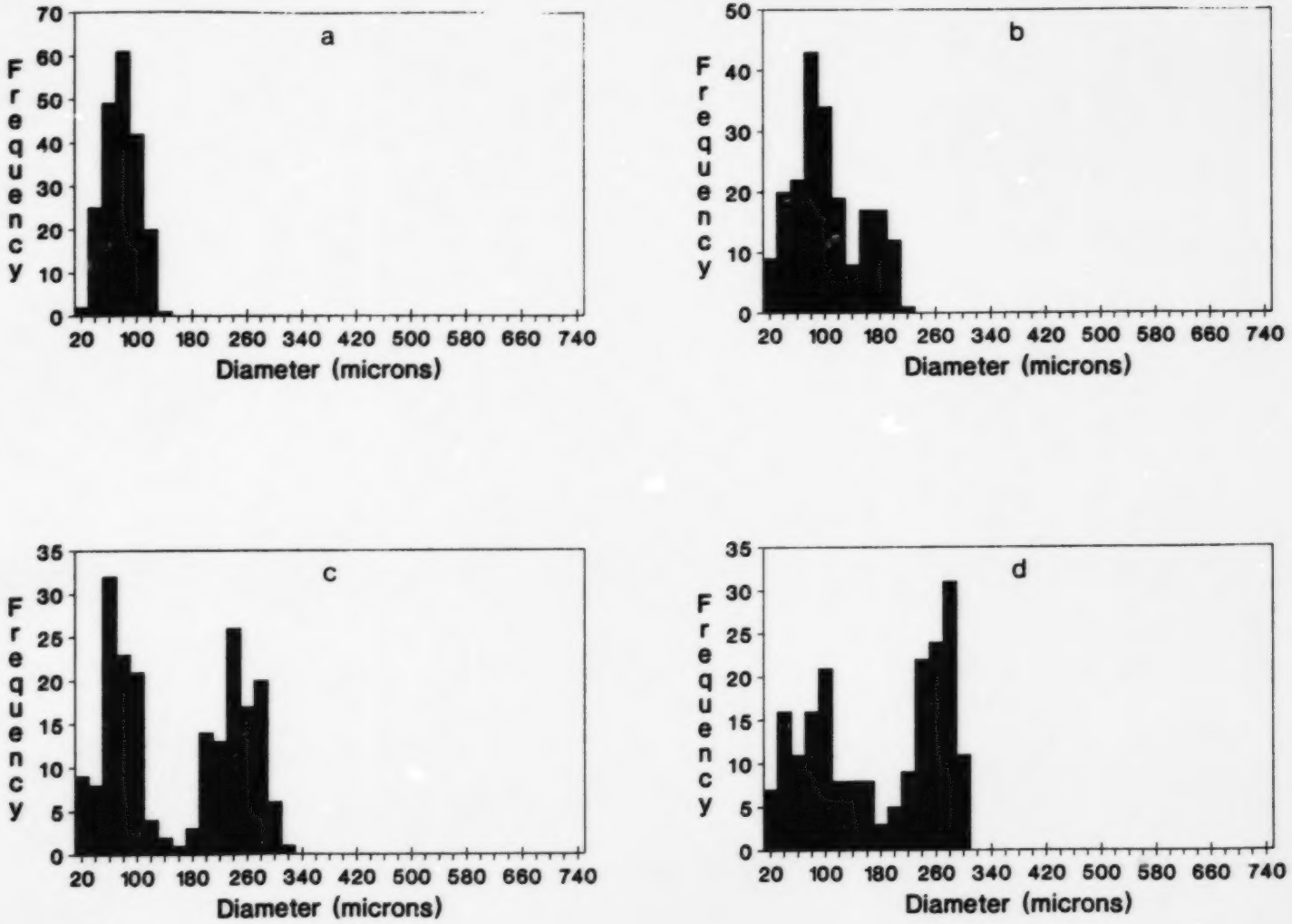
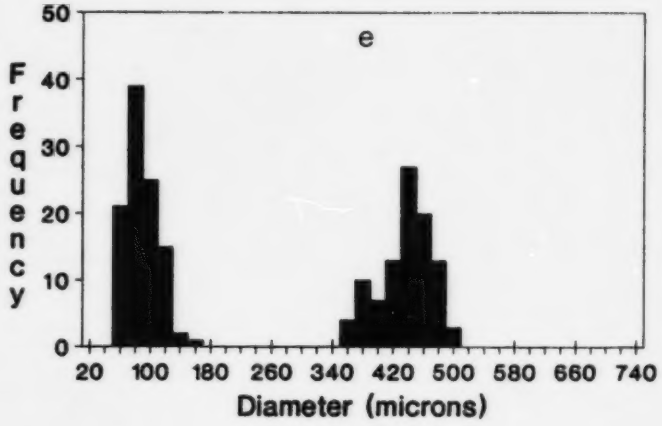
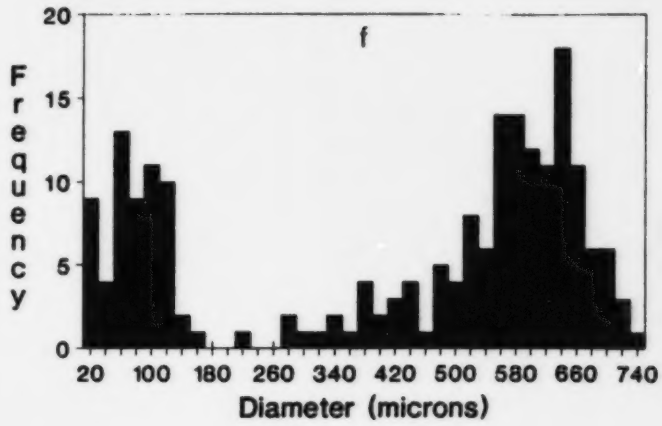
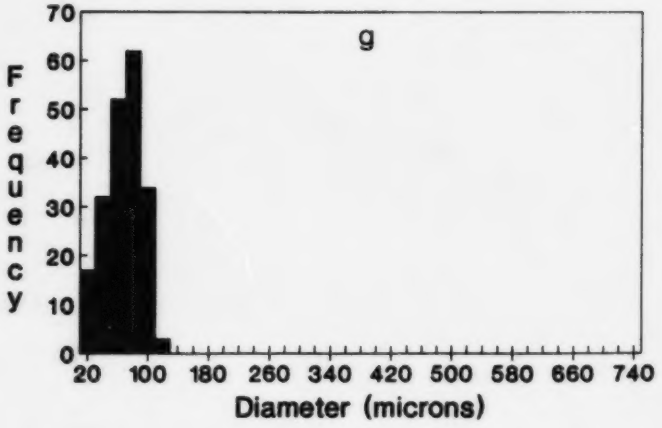


Figure 6. Frequency distributions of oocyte diameters. a) Stage 1, Fish no. 10. b) Early stage 2, Fish no. 4. c) Late stage 2, Fish no. 6. d) Stage 3, Fish no. 57.







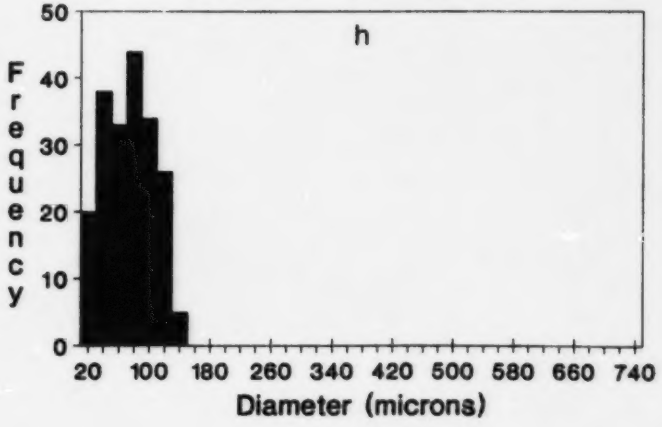


Figure 6 (cont'd). e) Early stage 4, Fish no. 26. f) Late stage 4, Fish no. 1. g) Early stage 6, Fish no. 16. h) Late stage 6, Fish no. 37.

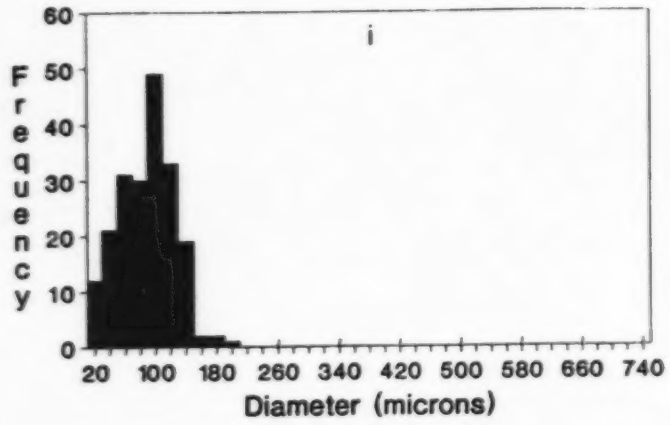


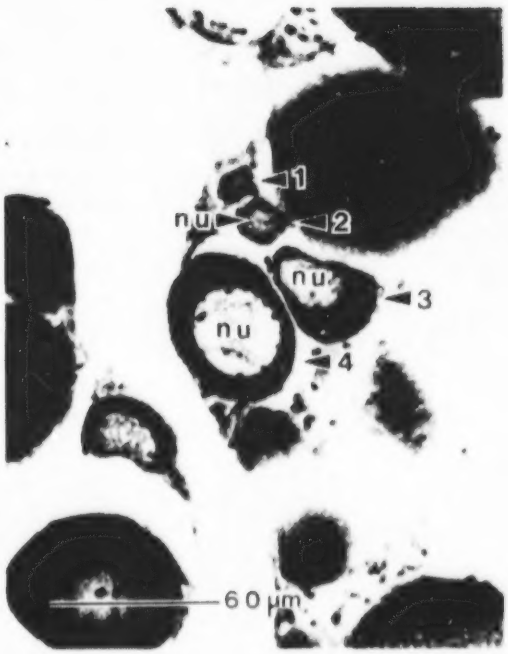
Figure 5 (cont'd). i) Stage 7, Fish no. 9.

Figure 7a. Oogonia and small reserve-fund oocytes. Fish no. 10. (1)&(2) oogonial cells with large, central nuclei (nu), (3) small oocyte with nucleus (nu) to one side, (4) small oocyte with central nucleus.

Figure 7b. Medium sized reserve-fund oocytes. Fish no. 10. (cy) cytoplasm, (en) euvitelline nucleolus, (nu) nucleus.

Figure 7c. Large reserve-fund oocytes. FIsh no. 10. Arrows indicate peripheral euvitelline nucleoli, (nu) nucleus.

Figure 7d. Early vacuolating oocytes. Fish no. 4. (cy) cytoplasm, (en) euvitelline nucleolus, (ex) external oocyte membrane, (nu) nucleus, (vl) vacuole.



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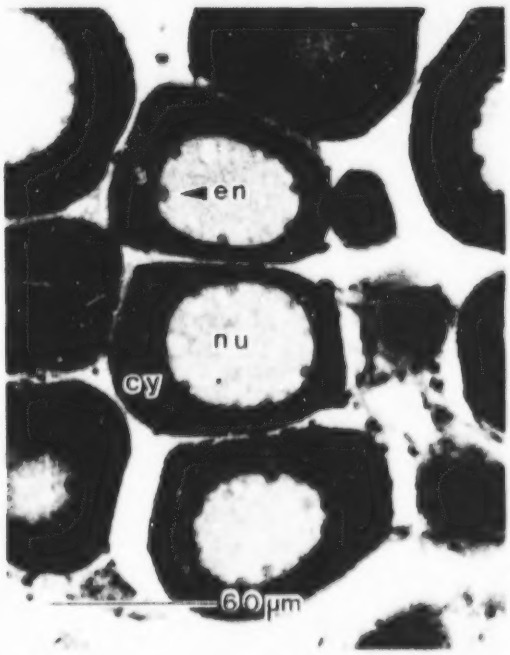

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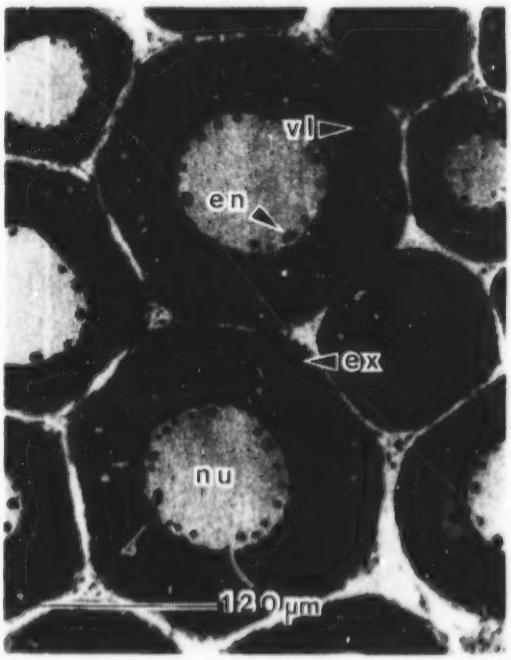

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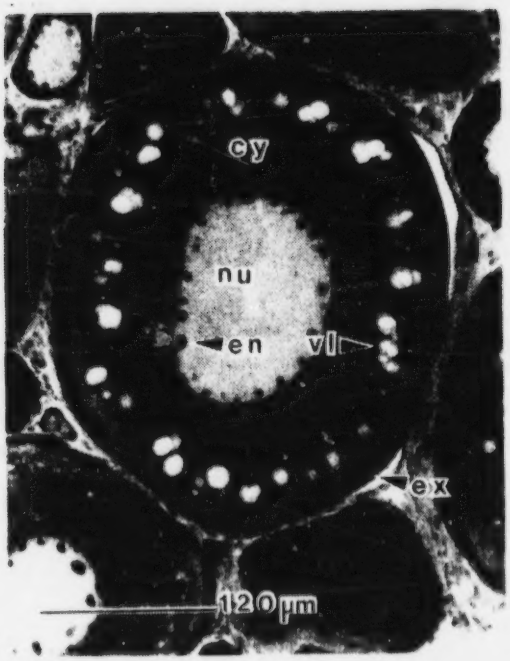
Figure 7e. Vacuolated oocyte. Fish no. 6.
(cy) cytoplasm, (en) euvitelline nucleolus, (ex) external oocyte membrane, (nu) nucleus, (vl) vacuoles.

Figure 7f. Oocyte with Balbiani's vitelline body. Fish no. 57.
(bv) Balbiani's vitelline body, (cy) cytoplasm, (en) euvitelline nucleolus, (ex) external oocyte membrane, (fc) follicle, (nu) nucleus, (vl) vacuoles.

Figure 7g. Early yolked oocyte. Fish no. 26.
(bv) Balbiani's vitelline body, (ex) external oocyte membrane, (fc) follicle, (nu) nucleus, (yg) yolk granules.

Figure 7h. Late yolked oocyte. Fish no. 1.
(en) euvitelline nucleolus, (ex) external oocyte membrane, (nu) nucleus, (yg) yolk granules.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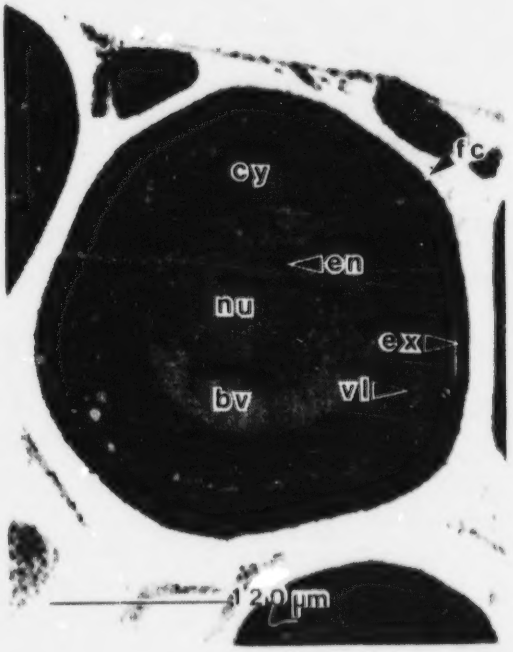
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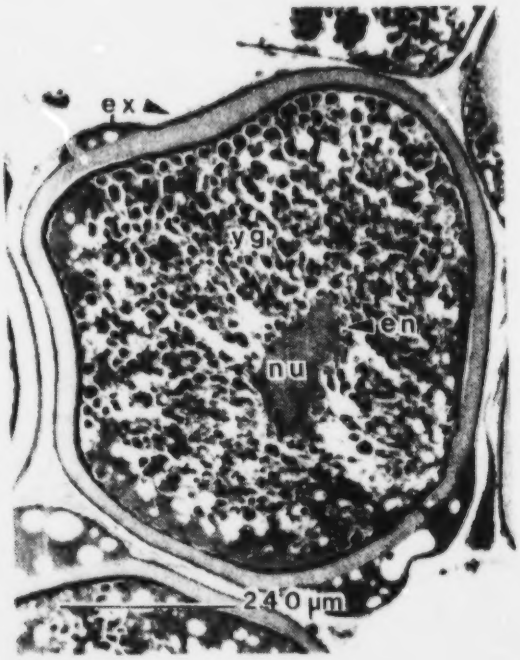
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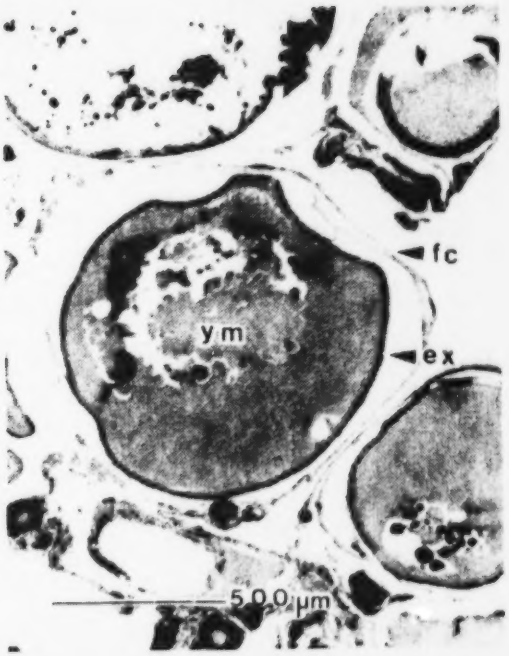
Figure 7i. Mature oocyte. Fish no. 23.
(ex) external egg membrane, (fc) follicle, (ym) yolk material.

Figure 7j. Resorbing oocyte. Fish no. 37.
(ex) external egg membrane, (fc) follicle, (mg) melanin granules.

Figure 7k. Resorbing oocyte. Fish no. 37.
arrows indicate characteristic invagination of the external oocyte membrane, (nu) nucleus.

Figure 7l. Atretic oocytes (bodies). Fish no. 37.
(ab) atretic body, (mg) melanin granules.



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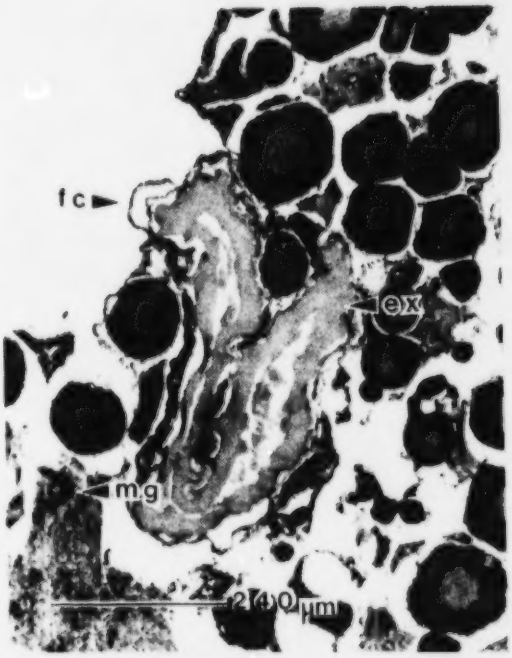

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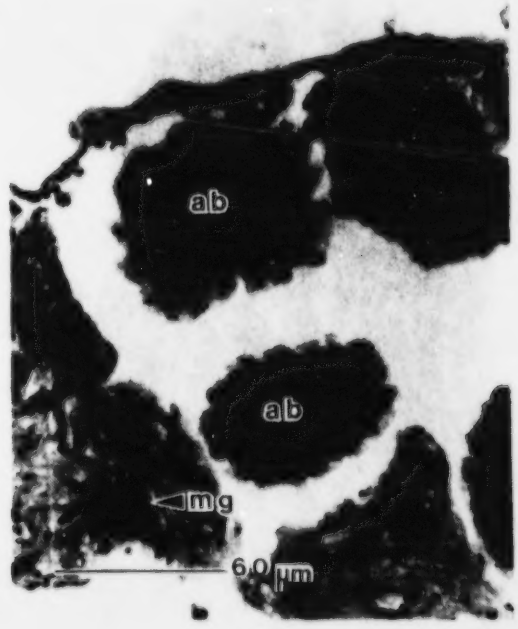

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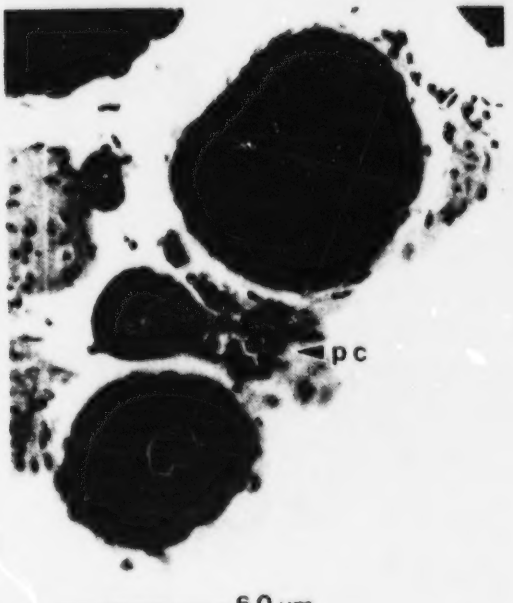
Figure 7m. Post synaptic cells (ps). Fish no. 37.

Figure 7n. Pycnotic cells (pc). Fish no. 37.

m



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GLOSSARY OF TERMS

The following glossary contains terms commonly encountered within the literature pertaining to fish reproduction and oogenesis.

Atresia: Process in which the follicle loses its nutritive role and takes on a possible endocrine function with resultant loss of the oocyte prior to ovulation (Byskov 1978).

Atretic body: The remains of a resorbed oocyte or ovum (Selyukov 1987).

Balbiani's vitelline body: A perinuclear complex of organelles and cellular inclusions of diverse morphology and chemical nature, which include mitochondria, phospholipid bodies, Golgi bodies and yolk granules. This so-called "yolk nucleus" in young oocytes develops adjacent to the nuclear envelope as a crescent of granular, basophilic substance (Guraya 1986). The function of the Balbiani's body is unclear, but may play a role in vitellogenesis (Detlaff and Vassetzky 1988). Also yolk nucleus.

Chorion: See external oocyte membrane (Robb 1982).

Corpora atretica: Degenerate follicle resulting from the process of atresia.

Corpora lutea: A structure derived from a resorbed follicle prior to ovulation (pre-ovulatory) or from an empty follicle after ovulation (post-ovulatory) (Foucher and Beamish 1977).

Egg capsule: See external oocyte membrane.

Egg envelope: See external oocyte membrane.

Egg membrane: See external oocyte membrane.

Egg shell: See external oocyte membrane.

Euvitelline nucleolus: One of several basophilic nucleoli found around the periphery of the nucleus of oocytes during the perinucleolar stage (Bell et al. 1986, Harder 1975). These nucleoli indicate the commencement of oocyte development (Robb 1982).

External oocyte membrane: The thick external covering enclosing the fluid-filled perivitelline space and oocyte. This membrane consists of three strata: the externus; the internus; and the subinternus. There are many terms used for the external oocyte membrane. This is pointed out by Groot and Alderdice (1985) who mention that "Commonly used terms for this outer covering of the egg include zona radiata, zona pellucida, chorion, radiate

membrane, egg membrane, primary membrane, vitelline membrane, vitelline envelope, egg envelope, egg shell, and egg capsule." Also ooplasmic membrane.

Follicular epithelium: See primary theca (Harder 1975).

Germ cells: Cells found in the outermost layer (germinal epithelium) of the immature ovary; that give rise to nests of oogonial cells by proliferation inwards (Harder 1975, Pennak 1964).

Germinal epithelium: The outermost layer of the immature ovary (Harder 1975). See germ cells.

Germinal vesicle: The greatly enlarged nucleus of an oocyte during prophase of the first meiotic division (Pennak 1964).

Granulosa: The inner of two follicular layers, enclosing a mature or maturing oocyte (Robb 1982). The granulosa, along with the primary theca or theca externa, provides nourishment to the oocyte via slender processes which associate with oocyte microvilli or radiate extensions (Groot and Alderdice 1984). Also theca interna.

Guanophore: See iridocyte (Harder 1975).

Iridocytes: Pigment cells often associated with the peritoneal membrane of the body cavity and viscera. Contain highly refractive guanine crystals giving a silvery appearance to the lining of the body cavity and viscera. Also guanophore (Harder 1975).

Lamellae: Extensions of the ovary wall which divide the lumen of the ovary into chambers. Lamellae are covered with germinal epithelium and provide a substrate for initial oocyte development (Harder 1975). Also ovigerous lamella, and septum.

Lumen: The internal cavity of the ovary (Harder 1975, Robb 1982). Also ovocoel.

Melanin granule: One of many dark, organic granules found in association with macrophages. Following spawning, the ovary undergoes a period of resorption, during which macrophages clean out any cellular debris. The influx of vast numbers of these macrophages gives the ovary wall a black colour (personal communication from J. Bagshaw, histologist, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.). See also iridocyte.

Microvillus: See plasmodesm.

Nonviable oocyte: An oocyte that has not reached full maturity prior to spawning. Such oocytes are resorbed (Foucher and Beamish 1980).

Oocyte: A cell derived from a mature oogonial cell; undergoes meiotic division to eventually produce an ovum. (Pennak 1964). See also primary and secondary oocyte.

Oogonium: Develops from a primordial germinal cell during the multiplicative phase. Oogonia continue to divide mitotically and enter a growth phase whereby they become oocytes (Harder 1975).

Ooplasm: The cytoplasm of an oocyte or ovum.

Ooplasmic membrane: See external oocyte membrane.

Ovigerous lamellae: See lamellae. (Foucher and Beamish 1977).

Ovocoel: See lumen (Aravindan and Padmanabhan 1972).

Ovum: A secondary oocyte which has undergone the second meiotic division and is haploid (Foucher and Beamish 1977).

Perivitelline space: The fluid-filled space between the oocyte and the external oocyte membrane (Groot and Alderdice 1985).

Plasmodesm or plasmodesmata: The protoplasmic extensions between cells, such as those of the follicular epithelium which play a role in intercellular communication (Harder 1975).

Primary membrane: See external oocyte membrane.

Primary oocyte: The smallest and youngest oocyte stage that develops from an oogonium. These oocytes are in the first stage of meiosis (synapsis) and are still diploid (Foucher and Beamish 1977).

Primary theca: The single layered follicle of an immature oocyte (Robb 1982). Also follicular epithelium.

Radiate extension: See plasmodesm.

Radiate membrane: See external oocyte membrane.

Reserve fund: Cells roughly 50-150 microns in diameter and containing no yolk. These cells represent the reserve stock of oocytes from which, each year, a proportion proceed with further growth and maturation (Foucher and Beamish 1980).

Resting oocyte: See reserve fund.

Secondary oocyte: Produced from the first meiotic division, the separation of homologous chromosomes of a resting or primary oocyte. Following ovulation, a secondary oocyte undergoes the second meiotic division to produce a haploid ovum (Foucher and Beamish 1977).

Septa: See lamellae (Robb 1982).

Theca externa: See primary theca. (Guraya 1986).

Theca interna: See granulosa. (Guraya 1986).

Tunica albuginea: The thick layer of mesenchymal tissue and muscle fibres beneath the outermost peritoneal membrane of the ovary (Aravindan and Padmanabhan 1972).

Vitelline envelope: See external oocyte membrane.

Vitelline membrane: See external oocyte membrane.

Vitellogenesis: The process of yolk formation and deposition (Detlaff and Vassetzky 1988).

Yolk nucleus: See Balbiani's vitelline body (Guraya 1986).

Zona pellucida: See external oocyte membrane.

Zona radiata: See external oocyte membrane.